PHALACROPSIS DISPAR (COLEOPTERA: PHALACRIDAE), AN ELEMENT IN THE NATURAL CONTROL OF NATIVE PINE STEM RUST FUNGI IN THE WESTERN UNITED STATES[1]

David L. Nelson[2]

Abstract.— Larvae of the phalacrid beetle *Phalacropsis dispar* (LeConte) consumed aeciospores and the underlying sporogenous mycelium, thereby destroying the aecia of all native western pine stem rust fungi studied. Aecia of the introduced white pine blister rust fungus (*Cronartium ribicola*) were not found to be infested by the beetle. A close, if not obligate, biosis of the beetle apparently exists with the native rust fungi, and their geographic distributions closely coincide. Laboratory tests and field observations indicate that the beetle completes its life cycle in 30 to 40 days and apparently overwinters as an adult. Quantitative data on aeciospore inoculum destruction were beyond the means of this study; however, observations over a 12-year period evidenced widespread and extensive destruction of aeciospores. The beetle may be an effective element in the natural control of native pine stem rust fungi. Natural control by secondary organisms could significantly reduce the selective pressure for high host resistance in a naturally evolving host-parasite population.

Direct control of pine stem rust disease problems through application of chemicals and eradication of alternate hosts is usually expensive and of questionable effectiveness (Toko et al. 1967, Leaphart and Wicker 1968, Peterson and Jewel 1968, Carlson 1978). Various silvicultural methods (Peterson 1966, Van Arsdel 1961, Nighswander and Patton 1965, Krebill 1968) and selection for host resistance appear to be the most acceptable means to immediate and long-term control (Hanover 1966, Bingham et al. 1971, Hiratsuka and Powell 1976). Research on pine stem rust in the western United States has concentrated on the exotic white pine blister rust (*Cronartium ribicola* Fisch. in Rabenh.). The native rusts are currently not considered important enough to justify more than limited study. Natural control other than host resistance may be an important factor in allowing this option. Answers for low-cost control of conifer rust diseases considered important could come from study of the natural control of native rust fungi. This may be especially true in the less extensively managed forests of western North America.

Host tissue affected by pine stem rusts and the fruiting bodies of the aecial state of the rust fungi provide an attractive habitat and food source for many other organisms. These are mainly fungi (Mielke 1933, Wollenweber 1934, Powell 1971a,b,c, Byler et al. 1972b, Williams 1972, Kuhlman and Miller 1976, Kuhlman et al. 1976, Hiratsuka et al. 1979, Tsuneda and Hiratsuka 1979, 1980, Tsuneda et al. 1980, Kuhlman 1981a,b), insects (Snell 1919, Myren 1964, Coulson and Franklin 1970, Powell 1971d,e, Furniss et al. 1972, Powell et al. 1972, Kuhlman 1981b), and, to a lesser extent, rodents (Mielke 1935, Powell 1974) and mollusks (Hunt 1978). They may play a more important role than is recognized in the selection and limitation of these rust fungi through reduction of aecial inoculum.

This study provides information on the identity, life history, and distribution of an aeciospore-consuming phalacrid beetle and suggests the possible importance of its destruction of aecia and the activity of other reported secondary organisms in the natural control of some western native pine stem rust fungi.

Review

Many insects and other arthropods are associated with pine stem and cone rusts in North America. Of special interest here are those that attack the rust fungi directly, are dependent upon them, consume large amounts of aeciospores, and consume or damage sporogenous mycelium.

[1]This article was written and prepared by a United States government employee on official time, and it is therefore in the public domain.

[2]Intermountain Forest and Range Experiment Station, Shrub Sciences Laboratory, Provo, Utah 84601. The initial observations for this study were made while the author was a student at the University of California, Berkeley.

Hubert (1923) described the activity of *Epuraea ovata* Horn (Coleoptera: Nitidulidae) larvae as consuming the entire aeciospore mass and underlying stromatic mycelium of the western gall rust fungus, *Endocronartium harknessii* (*Peridermium harknessii*). Powell (1971d) reviewed insects associated with pine stem rusts and listed 160 species of arthropods he found on *Cronartium comandrae* blister rust cankers on *Pinus contorta* Dougl. Powell et al. (1972) listed those found associated with *E. harknessii, C. comandrae, C. coleosporioides,* and *C. comptoniae* Arth. Using Graves's and Benick's system of classification, Powell (1971d) classed *Epuraea obliquus* Hatch, *Paracacoxenus gluttatus* Haryd & Wheeler (Diptera: Drosophilidae), and a mite, *Diapterobates principalis* Berlese (Acarina: Ceratozetidae), as apparent true mycetobionts completely dependent on the aecia of *C. comandrae* for food. *Epuraea obliquus* was also found associated with *C. coleosporioides, Endocronartium harknessii,* and *C. comptoniae* (Powell et al. 1972). Species of 12 genera of the insect orders Homoptera, Coleoptera, Lepidoptera, and Diptera associated with comandra blister rust (*C. comandrae*) cankers were considered to be apparent facultative mycetophiles. Several species of the mycetophilous type, especially the cone moth *Dioryctria* spp. (Lepidoptera: Pyralidae), extensively damaged areas of the aecial and spermogonial zone by burrowing in infected phloem tissue. Similar behavior of this moth has been observed on *C. fusiforme* Hedgc. & Hunt (Coulson and Franklin 1970), *C. strobilinum* (Arth.) Peterson (Merkel 1958), *C. comptoniae* (Anderson and French 1964), *E. harknessii* (Byler et al. 1972a), and *C. coleosporioides* (Powell 1971d). Powell (1971d) regarded most of the 38 species of Hymenoptera he observed as parasitic on Lepidoptera, Diptera, and Coleoptera that inhabited the rust cankers. Furniss et al. (1972), examining cankers of white pine blister rust in northern Idaho, found some of the species described by Powell (1971d) and Powell et al. (1972), but the number and diversity of species were considerably less. The only apparent true mycetobiont type found by Furniss et al. was *Paracacoxenus gluttatus*.

The extent to which pine stem rusts are damaged by these insects has received little study, and the impact of insect attacks on reduction of aeciospore inoculum and on subsequent infection of pine has received even less. Over a seven-year period, between 32 and 57 percent of the *C. comandrae* cankers received obvious annual damage on 23 locations, according to Powell (1971b). From 60 to 80 percent of the cankers were damaged yearly over this period. Insects infested up to 49 percent of recently dead or damaged galls of *E. harknessii* on *Pinus radiata* D. Don on one plot in California (Byler et al. 1972a). Nearly 45 percent of the *E. harknessii* galls studied by Wong (1972) in Manitoba and Saskatchewan over a four-year period were mined by larvae of *Dioryctria banksiella* Mutuura, Munroe, and Ross, but Wong gave no information on damage to the rust fungus. Attacks by some insects that consume aeciospores can be severe. Studies in southwestern Alberta (Powell 1971d) indicated a yearly 10 percent reduction in aeciospore production, with some years having a much higher percentage. *Epuraea obliquus* occurred on as many as 80 percent of the sporulating cankers on a single location, with at least 50 percent being attacked over a five-year period. Dipterous and lepidopterous larvae were observed on over 25 percent of sporulating cankers in certain locations. The activity of *Dioryctria* sp., *E. lengi* Parsons, unknown dipterous larvae, and other insects apparently was of little importance in reducing aeciospore inoculum of southern fusiform rust in North Carolina according to Kuhlman (1981b).

METHODS

During other research on native western conifer rusts, a beetle was frequently observed in the aecia of pine stem rust fungi. The beetle's distribution and activity were studied on annual field trips from 1963 through 1975. Observations were made in coastal California from Fort Bragg south to the San Francisco Bay area and the Sierra Nevada, western Nevada from Lake Tahoe south to the Spring Mountains north of Las Vegas, northern Arizona south to Prescott, most of Utah, extreme western Wyoming,

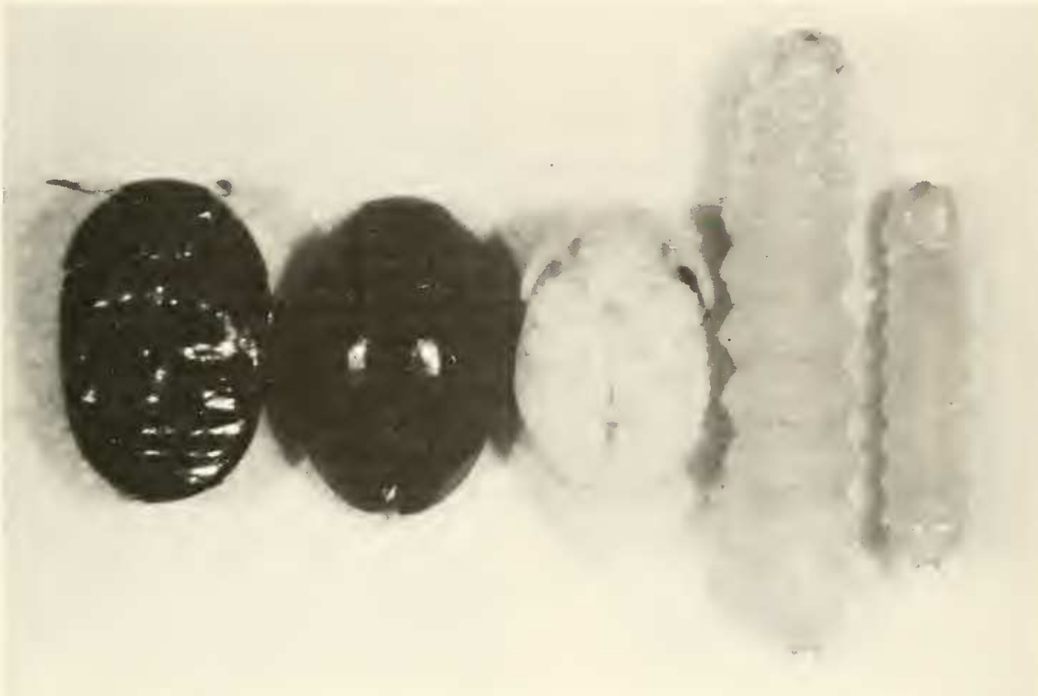

Fig. 1. Adult, pupal, and larval stages of *Phalacropsis dispar,* enlarged 14 times.

southern Idaho from the Salmon River south, and east central Oregon.

Because of the uncertain taxonomic status of some of the rust fungi involved and because the study is concerned with the aecial state, the imperfect or peridermium name of some of the rust fungi will be used for clarity throughout the remainder of the paper.

To obtain information on beetle life history, rust-infected stem sections that were also beetle infested were collected for laboratory study. Infested rust samples were placed in one-liter glass beakers for observation. Drying of specimens was slowed by covering beaker tops with a plastic film punctured in several places to allow air exchange. Cheesecloth was placed over the film to prevent escape of insects. Thus assembled, the specimens were held in the laboratory at normal room temperature, approximately 21 C. Both natural and fluorescent light was received during the day. Observations on development were made daily when possible. Dates when larvae matured, pupation began, and adult beetles emerged were recorded.

Three locations were selected for annual field observation of beetle activity and rust development: (1) Bucks Lake, Plumas National Forest, Plumas County, California; (2) Lee Vining Creek, Toiyabe National Forest, Inyo County, California; and (3) Red Canyon, Dixie National Forest, Garfield County, Utah. At location one, western gall rust, caused by *Peridermium harknessii* (*Endocronartium harknessii*), was present on *Pinus ponderosa* Laws.; at location two, limb rust and stalactiform canker rust (both caused by *Peridermium stalactiforme* [Peterson 1968], an imperfect state of *Cronartium coleosporioides*), were present on *Pinus jeffreyi* Grev. & Balf. and *P. contorta*, respectively; and at location three, Powell limb rust (Peterson 1968), caused by *Peridermium filamentosum*, was present on *Pinus ponderosa.* Observations were made at location one from 1963 through 1975 and at locations two and three from 1967 through 1975. These locations were visited one to three or more times each year during the aecial sporulation period.

RESULTS

Habitat and Identification

Numerous small, white-to-grayish beetle larvae (Fig. 1) were frequently found in the

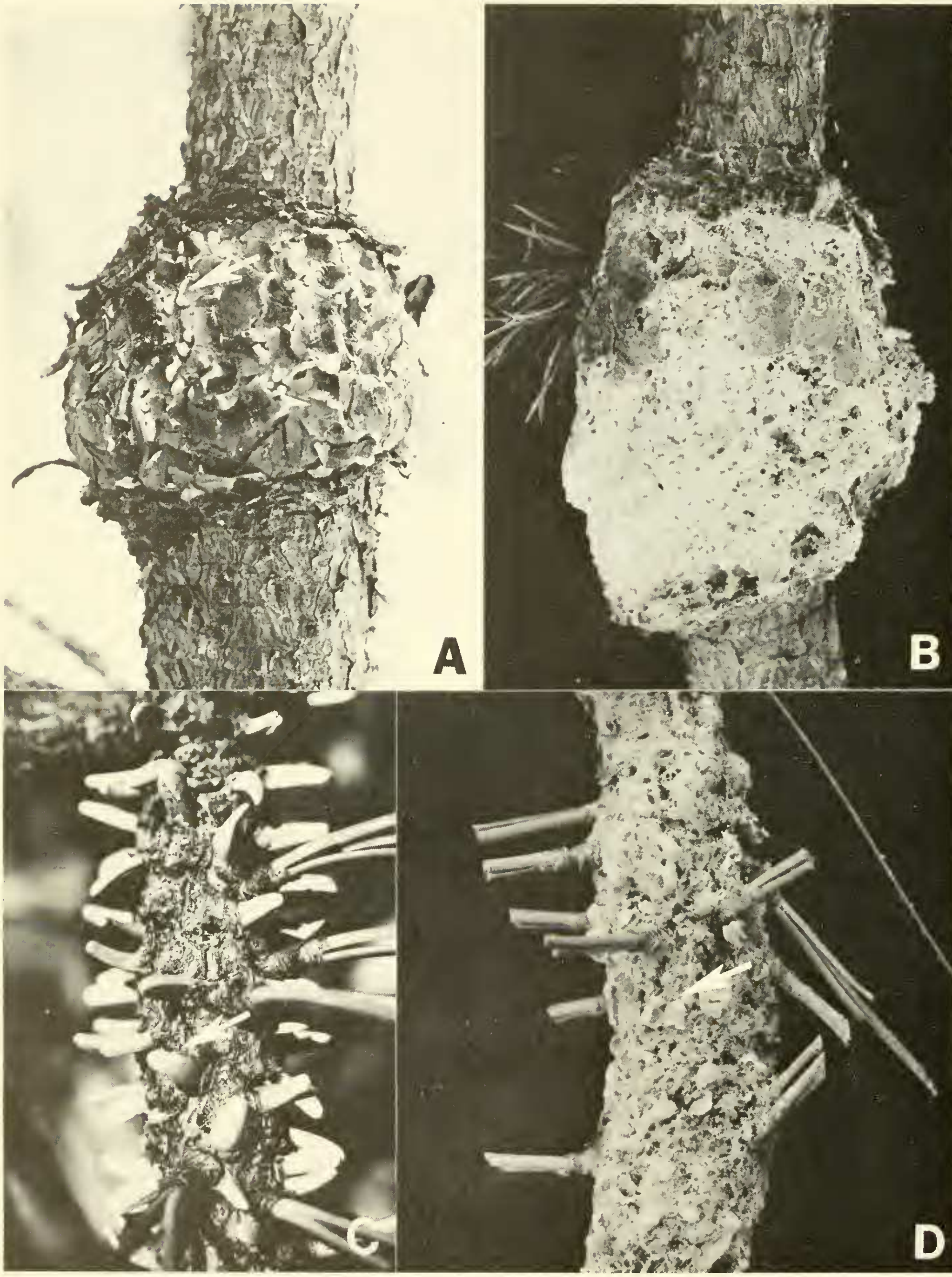

Fig. 2. Beetle-damaged pine stem rusts (note weblike fecal debris over surface of stems): western gall rust (A) unopened, uninfested aecia (arrow) one-half actual size; (B) insect-damaged aecia; limb rust (C) unopened, uninfested aecia (arrow) actual size; (D) insect-damaged aecia (arrow points to unconsumed peridial fragments).

aecial spore masses (Fig. 2A–D) of the various pine stem rust fungi observed. Their voracious consumption of aeciospores and of the underlying sporogenous mycelium effectively reduced aecia (Fig. 2A, C) to a mass of fecal debris within several weeks' time (Fig. 2B, D). Microscopic examination of young larvae revealed that the gut and intestinal tract were full of aeciospores. Masses of spores were discharged in strings of fecal pellets. Several germination tests of aeciospores from fecal pellets failed to show any viability. Unconsumed spores in the same collections germinated. Spores of secondary fungi (such as *Penicillium*, which commonly invade aecial masses [Byler et al. 1972a]) were also consumed by the larvae. The peridium of aecia was not consumed.

Beetle specimens reared in the laboratory from larval-infested western gall and limb rust samples were used for identification. Larvae pupated and developed into shiny chestnut brown beetles about 3 mm in length (Fig. 1). They were identified as *Phalacropsis dispar* (LeConte) by Dr. Carl T. Parsons, who confirmed his identification by comparing specimens with the type specimen at the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

Phalacropsis is a monotypic genus described by T. L. Casey (1889–1890). The type specimen was collected in 1878 by E. A. Schwarz on a geological survey at 9400 ft on Veta Pass, Colorado, and described by T. L. Le Conte (1879). No host plant was mentioned. *Phalacropsis dispar* apparently is rarely collected. A check of 20 insect museums throughout the United States revealed only six collections as follows: California Academy of Sciences, Golden Gate Park—two collections, both from the Sierra Nevada, one on *Pinus* sp., no host listed for the other specimen; Ohio State University—two collections, one from Yosemite National Park, California, the other from the Chiricahua Mountains of Arizona, no hosts were listed; and National Museum of Natural History—two collections, one from the Sitgreaves National Forest, Arizona, on *Pinus ponderosa* and the other from Pringle, South Dakota, on *Peridermium harknessii* aecia. Mountainous locations and hosts from which the specimens were collected indicate they all could be from pine stem rust aecia. Specimens of *Phalacropsis dispar* collected during this study have been deposited in the Museum of Comparative Zoology (Agassiz Museum), Harvard University, and the National Museum of Natural History Smithsonian Institution, Washington, D.C.

Distribution

The distribution of *P. dispar* observed in this study is indicated in Figure 3 and Table 1. With few exceptions, the beetle was found wherever pine stem rust fungi were examined closely during the aecial sporulation period. The most intensive study was made in Utah and in the Sierra Nevada of California, and the number of sites for the beetle in these areas (Fig. 3) is a reflection of this and is not necessarily an indication of abundance.

During a five-year study of western gall rust on pines in coastal areas of California, *P. dispar* was not encountered, nor was it listed by Byler et al. (1972a), who studied the same rust in these areas. In north coastal California near Fort Bragg, however, an unidentified larva of similar habit was abundant in aecia of *Peridermium harknessii* on *Pinus contorta*

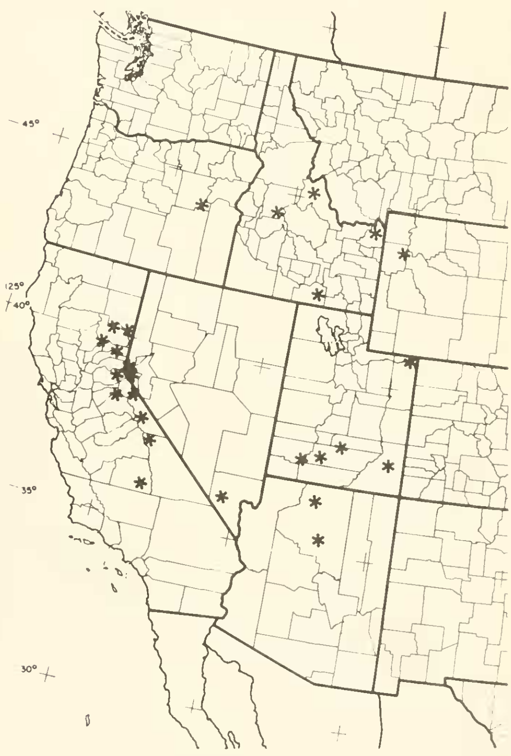

Fig. 3. Distribution of *Phalacropsis dispar* observed in this study on pine stem rust fungi in the western United States.

ssp. *bolanderi* (Parl.). Several attempts to rear adults failed. In the Sierra Nevada, *Phalacropsis dispar* was found on *Peridermium filamentosum* Inyo form (Peterson 1968), *P. stalactiforme* both forms, *P. harknessii*, *Cronartium occidentale*, and "Bethel" blister rust (Dixon 1978) (Table 1). *Cronartium comandrae* was not studied in this area. In the Bucks Lake area, *Phalacropsis dispar* was not found in aecia of the introduced *C. ribicola* on *Pinus lambertiana* (Dougl.). In this area, the *C. ribicola*-infected *P. lambertiana* occurred in several stands that were intermixed with *Peridermium harknessii*-infected *Pinus ponderosa* and *P. contorta*. The aecia of *Peridermium harknessii* on these pines were infested with *Phalacropsis dispar*. In the Spring Mountains of southern Nevada, *P. dispar* was found on the Coronado and Powell (Peterson 1968) forms of *Peridermium filamentosum* limb rust and was especially abundant on the albino form (Mielke and Peterson 1967) of western gall rust on *Pinus ponderosa*. In Arizona, *Phalacropsis dispar* was observed on the Coronado and Powell forms of *Peridermium filamentosum* limb rust on *Pinus ponderosa* on the Kaibab Plateau and in the San Francisco Mountains. In Utah, *Phalacropsis dispar* occurred on the Coronado and Powell forms of *Peridermium filamentosum* limb rust on *Pinus ponderosa* in the Abajo Mountains and on the Aquarius and Markagunt Plateaus in the southern end of the state. It also occurred on the Powell *Peridermium filamentosum* limb rust on *Pinus ponderosa* at the eastern end of the Uinta Mountains in northeastern Utah. It was not found on *C. comandrae*, *Peridermium harknessii*, and *P. stalactiforme* on *Pinus contorta* in the Wasatch Mountains of northern Utah. *Phalacropsis dispar* was found—although rarely—on *C. comandrae* on *Pinus contorta* on the Cassia Plateau of southern Idaho and on the northern end of the Wind River Range in western Wyoming. It occurred in *Peridermium harknessii* aecia on *Pinus contorta* in the Island Park area of eastern Idaho and on the same rust on both *P. contorta* and *P. ponderosa* in the Sawtooth Mountains in the south central part of the state. It was found

TABLE 1. The *Peridermium* species of pine stem rust fungi found in this study to be infested by *Phalacropsis dispar* in the western United States.

Peridermium rust	Pine host	Location
Cronartium coleosporioides Arth.		
Peridermium filamentosum Peck		
Coronado limb rust	*Pinus ponderosa*	Arizona, Nevada, Utah
Powell limb rust	*Pinus ponderosa*	Arizona, Nevada, Utah
Inyo limb rust	*Pinus jeffreyi*	California
Peridermium stalactiforme Arthur & Kern		
Stalactiforme limb rust	*Pinus jeffreyi*	California, Nevada
Stalactiforme canker rust	*Pinus contorta*	California, Oregon
	Pinus ponderosa	Idaho
Endocronartium harknessii (J. P. Moore) Y. Hiratsuka		
(*Peridermium harknessii* J. P. Moore)		
Western gall rust	*Pinus contorta*	California, Idaho, Oregon
	Pinus ponderosa	California, Idaho
Albino western gall rust	*Pinus ponderosa*	Nevada, Utah
Cronartium comandrae Peck		
Peridermium pyriforme Peck		
Comandra blister rust	*Pinus contorta*	Idaho, Wyoming
"Bethel" blister rust	*Pinus contorta*	California
Cronartium occidentale Hedg., Bethel, & Hunt		
Peridermium occidentale Hedg., Bethel, & Hunt		
Pinyon blister rust	*Pinus monophylla*	California

on a single canker of *Peridermium stalactiforme* on *Pinus ponderosa* in the Salmon River Mountains. In the Malheur National Forest of Oregon, *Phalacropsis dispar* was found on *Peridermium harknessii* and *P. stalactiforme* on *Pinus contorta*. In the central Idaho and Oregon areas mentioned, larvae and adults of an *Epuraea* sp. (another aeciospore-consuming beetle) were also present. From northern Utah northward, occurrence of *Phalacropsis dispar* was less frequent to rare and southward from this point it was increasingly abundant.

Life History Observations

Phalacropsis dispar was first noted in mid-May near Bucks Lake and in late May at Lee Vining and Red Canyon. Aecia of the associated rust fungi were just beginning to appear through the bark. On sunny days, adult beetles were seen on rusted limbs, crawling about and copulating. Egg-laying by the beetle was observed only in association with *Peridermium filamentosum* on *Pinus jeffreyi* in the Sierra Nevada of California. Single eggs were deposited at the exterior base of aecia. Larval activity began before full development of aecia and well in advance of peridial rupture. With the beginning of aeciospore release, larval activity had reached a peak. Beyond this stage, in the case of early sporulating rust fungi, adult beetles were not seen on rusted limbs; however, in the case of later sporulating Powell and Inyo forms of *Peridermium filamentosum*, adults were seen throughout July and August well after aecial maturity. After larval maturity, the insect disappeared from rusted limbs and galls and possibly pupated in the needle duff at the base of trees. Whether or not the insect overwinters in the pupal or adult stage in its natural environment was not studied.

In laboratory tests (Table 2), rusted stems were collected 10 to 15 days after adults were first seen. The first larvae began moving from aecia about 6 days after rust specimens were placed in glass beakers in the laboratory. Pupation began 4 to 7 days later on the floor of the beaker under masses of fecal debris, unconsumed aeciospores, and bark fragments that dropped from rusted stems. Beginning of pupation was determined by a shortening and thickening of larvae, their immobility, and the appearance of black eye spots. The first adults emerged 14 to 36 (average 23) days after the first larvae began leaving aecia. If development proceeds similarly under natural conditions, roughly 30 to 40 days would be required for completion of the beetle's life cycle.

The beetles were not found on other plants in the vicinity of the pine stem rusts, although members of the family Phalacridae are known to frequent flowers of the Compositae in particular (Arnett 1973).

Beetle Infestations and Damage

At the Bucks Lake location where *P. harknessii* occurred on *Pinus ponderosa*, several hundred galls were observed annually on a stand of young trees covering approximately 0.5 ha. During the entire study period, not a

TABLE 2. Incubation period of *Phalacropsis dispar* in laboratory tests.

Year	National forest	Rust[1] fungus pine host	Collection date	Placed in beaker	Larvae moving from aecia	Pupation began	First adults	Total days from first larval maturity
1967	Toiyabe, California	Ps/Pj	7/14	7/17	7/20	7/24	8/3	14
1968	Toiyabe, California	Ps/Pj	6/22	6/25	7/1	7/5	7/17	16
1969	Dixie, Utah	Pf/Pp	6/23	6/25	7/3	7/22	7/28	25
1970	Plumas, California	Ph/Pp	5/26	5/28	6/3	6/18	6/29	26
1971	Plumas, California	Ph/Pp	5/30	6/6	6/12	6/16	7/14	36
1973	Plumas, California	Ph/Pp	5/28	5/28	6/4	6/11	6/26	22
1974	Plumas, California	Ph/Pp	5/23	5/25	5/31	6/4	6/18	18
1975	Toiyabe, Nevada	Pha/Pp	7/12	7/13	7/18	7/25	8/6	19

Ps/Pj = *Peridermium stalactiforme/Pinus jeffreyi*
Pf/Pp = *Peridermium filamentosum/Pinus ponderosa*
Ph/Pp = *Peridermium harknessii/Pinus ponderosa*
Pha/Pp = *Peridermium harknessii* (albino)/*Pinus ponderosa*

single gall was found without some evidence of beetle larval activity. Larvae reduced aeciospores and the underlying sporogenous mycelium to a mass of fecal debris (Fig. 2B) within approximately two weeks. The initial sporulation of young galls is usually a week or so later than older galls; these also become infested. In a single laboratory test (1971), four galls, 4 to 8 cm in diameter, produced an average of 130 adult beetles per gall.

A beetle infestation of similar intensity occurred on *Peridermium stalactiforme* on *Pinus jeffreyi* at Lee Vining Creek. Aecia matured about mid-June and were completely destroyed within about two weeks. Along a three km stretch of Lee Vining Creek, not one of the 20 limb-rusted trees examined annually remained free of the beetle. Aecial confluency with this rust is markedly less than with western gall rust, but few aecia were uninfested. Those that were uninfested were the more scattered aecia among needles toward the distal end of limbs. In two laboratory tests (1968 and 1971), a total of 3.9 m of typical rusted limbs yielded 3.4 adult beetles/cm and a total of 4.6 m of rusted limbs yielded 1.2 beetles/cm.

Beetle infestation of the Powell *Peridermium filamentosum* studied at Red Canyon was somewhat different from the infestations of *P. harknessii* and *P. stalactiforme* described above. With this rust fungus, aecia are tongue shaped and single with little confluency (compare Figs. 2A and 2C). Seldom did more than one beetle larva occur within a single aecium. Larvae consumed the basal mycelium of an aecium first and then moved into the upper part. Frequently the upper part of aecia remained untouched. Pressure from the growing fecal mass often burst the aecium at its base. It appeared that a single aecial mass was sufficient to rear a single larva. Usually, fewer than 50 percent of the aecia became infected on rusted limbs of the 12 trees observed annually. The amount of damage seemed to vary more from year to year with this rust than with *P. harknessii* and *P. stalactiforme*. In California, few Inyo *P. filamentosum* aecia were infested some years, but virtually all aecia became infested in other years.

The other pine stem rusts were studied less. Infestation of *P. stalactiforme* on *Pinus contorta* in the Sierra Nevada of California was as severe as that noted on *P. jeffreyi* at Lee Vining Creek. Infestation of the Coronado *Peridermium filamentosum* was similar to that of the other forms of *P. filamentosum*, although limited to a shorter sporulation period. *Cronartium comandrae* was studied little, and so the extent of infestation was not known. Observation of the beetle on *C. occidentale* on *Pinus monophylla* Torr. and Frem. was limited to a large outbreak of the rust near Monitor Pass, Alpine County, in the Sierra Nevada of California. During the three seasons observed, aecial spore masses were virtually destroyed by the beetle in all trees examined.

Discussion

The beetle *Phalacropsis dispar* is reported here to consume the aeciospores and the aecial mycelium of all species of native western pine stem rust fungi except *Cronartium conigenum* (Pat.) Peterson and *C. comptoniae*, neither of which was investigated. Aecial fructifications not only provide food but also protective chambers for the larvae. Within several weeks' time, aecia may be completely ravaged of their content; only the peridial shell and masses of fecal debris remain. Based on laboratory tests and field observations, the life cycle of the beetle is completed in 30 to 40 days. Apparently, the beetle overwinters as an adult and emerges in the spring to mate and lay eggs as aecia of the rust fungi begin forming. The rarity of *P. dispar* in insect collections is further evidence it is highly specific to these rust fungi. The insects are abundant on pine stem rust fungi, but these fungi are rather obscure to insect collectors. Also, if they live on other fungi or the flowers of vascular plants as do other Phalacaridae, they probably would turn up more frequently in collections.

The distribution of *P. dispar* appears to be primarily south of the 40th parallel. North of the parallel, the niche becomes increasingly occupied by *Epuraea* spp. Some adults or larvae of *P. dispar* could be found in almost all areas where native pine stem rust fungi in the aecial sporulation state were studied. The beetle appeared, however, to be absent in some areas such as coastal California and northern Utah. R. S. Peterson (pers. comm.) has found *Phalacropsis* to be common to abundant on both the albino and orange-spored *Peridermium harknessii* in the Black Hills of South Dakota and Wyoming and in parts of Colorado.

Reduction of the aeciospore inoculum by *Phalacropsis dispar* was not determined in quantitative terms, but based on my observations, it can be a high percentage of the potential amount. Not only is there a reduction of spores already formed at the time larvae begin feeding, but consumption of the underlying sporogenous mycelium reduces the final quantity of spores produced as well as the length of the sporulation period. Quantitative field data are needed to establish what impact *P. dispar* has in reducing aeciospore inoculum and in the natural control of pine stem rust fungi. Nevertheless, all factors in the host-pathogen-environment interaction are of some importance.

Information on the aeciospore dispersal period for native western pine stem rust fungi is limited. R. S. Peterson (1959), studying spore release from *Peridermium harknessii* at high elevation sites in Colorado, found intermittent, but abundant, sporulation for one to two months. In a two-year study, G. W. Peterson (1973) trapped 88 and 91 percent of the season's total release of *P. harknessii* aeciospores during a two- and three-week period each May. The remainder (9 to 12 percent) was trapped through June. In Krebills's (1968) study of *C. comandrae* in the Rocky Mountain States, aeciospore dispersal began in late May, peaked in the last half of June, and usually continued in small amounts through summer. With increasing elevation, dispersal was delayed and the period shortened.

The tremendous mass of spores produced by the aecial state of the pine stem rust fungi is an evolutionary adaptation that increases the chance for survival of these propagules through the environmental hazards of dissemination. Aeciospores (annual inoculum) serve as the initial step in what is a long series of events leading to infection of pine. They also function in the spread of rust fungi over long distances, and a reduction in the inoculum load would seem to be important. In autoecious rust fungi, such as *Endocronartium harknessii* (*Peridermium harknessii*), reduction of the aecial inoculum is likely to be of more significance than it would be in heteroecious rust fungi, such as *C. coleosporioides* or *C. comandrae*, which have the uredinial multiplication phase. The Inyo and Powell forms of *P. filamentosum*, with aecia adapted to survive potentially long dry periods, could be severely affected by early destruction of aecia. Even with heteroecious rust fungi, in the more arid regions of the western United States where favorable moisture requirements for infection are likely to occur less frequently during the uredinial phase, intensity of infection by aeciospores would seem to be important. *Phalacropsis dispar* is possibly specific to native conifer stem rust fungi, including *C. occidentale*, which is similar in host range to *C. ribicola*. If *P. dispar* does not feed on the introduced *C. ribicola*, it may reveal a deficit in the natural control of this rust fungus in North America. From reports in the literature, there appears to be a larger diversity of secondary organisms that inhabit native western pine stem rusts (Wollenweber 1934, Powell 1971a,b,c,d,e, Byler et al. 1972b, Powell et al. 1972, Powell 1974, Hiratsuka et al. 1979, Tsuneda and Hiratsuka 1979, 1980) than inhabit *C. ribicola* blister rust (Mielke 1933, 1935, Kimmey 1969, Williams 1972, Furniss et al. 1972, Hungerford 1977, Hunt 1978). Members of the genus *Epuraea* evidently are widely distributed in the northwestern United States and western Canada (Hatch 1961, Parsons 1967, Powell 1971d, Powell et al. 1972). The aggressive *Epuraea obliquus* and *E. ovata*, obligate consumers of aeciospores of four different species of native pine stem rust fungi (Hubert 1923, Powell et al. 1972), were not reported by Furniss et al. (1972) to occur on *C. ribicola* blister rust cankers in northern Idaho. Both *E. obliquus* and *E. ovata* are known to exist in the eastern Oregon, northern Idaho, and western Montana areas (Hubert 1923, Hatch 1961). The absence of natural control of *C. ribicola* in western North America has been attributed primarily to a lack of host resistance (Bingham et al. 1971, Hoff and McDonald 1972). Byler et al. (1972a) provide evidence that secondary fungi and insects were primarily responsible for stabilizing populations of *Peridermium harknessii* at a low equilibrium position on coastal California pines. *Pinus radiata* and other coastal pine species become heavily infected with this rust fungus. Although these species are apparently highly susceptible to infection, resistance mechanisms probably provide tolerance (True 1938). Genetic drift of susceptibility from areas protected by an environment unfavorable for infection could account for part of this high susceptibility. The extent of natural control resulting from the activity of secondary organisms is a possible explanation for the reduced need for host resistance.

The rust fungi are well-known obligate parasites and have evolved with their hosts to a state of mutual survival. Considering the factors involved in rust disease epidemiology, it appears that secondary organisms would tend to reduce disease incidence and thus reduce selection for host resistance. The importance of secondary organisms should perhaps be placed more in the perspective of what disease incidence might be in their absence rather than as candidates for biological control above and beyond what occurs in a natural environment.

Literature Cited

Anderson, N. A., and D. W. French. 1964. Debarking jack pine infected with sweetfern rust. Plant Dis. Rept. 48:530–531.

Arnett, R. H., Jr. 1973. The beetles of the United States (A manual for identification). Amer. Entomol. Inst., Ann Arbor, Michigan. 1112 pp.

Bingham, R. T., R. J. Hoff, and G. I. McDonald. 1971. Disease resistance in forest trees. Ann. Rev. Phytopathol. 9:433–452.

Byler, J. W., F. W. Cobb, Jr., J. R. Parmeter, Jr. 1972a. Effects of secondary fungi on the epidemiology of western gall rust. Canadian J. Bot. 50:1061–1066.

———. 1972b. Occurrence and significance of fungi inhabiting galls caused by *Peridermium harknessii*. Canadian J. Bot. 50:1275–1282.

Carlson, C. E. 1978. Noneffectiveness of *Ribes* eradication as a control of white pine blister rust in Yellowstone National Park. USDA For. Serv. N. R. Rept. 78-18.

Casey, T. L. 1889–1890. Coleopterological notices. Ann. New York Acad. Sci. 5:89–144.

Coulson, R. N., and R. T. Franklin. 1970. The occurrence of *Dioryctria amatella* and other insects in *Cronartium fusiforme* cankers. Canadian Entomol. 102:353–357.

Dixon, C. S. 1978. A *Peridermium* rust associated with dwarf mistletoe on lodgepole pine. Unpublished thesis. Colorado State Univ. 100 pp.

Furniss, M. M., R. D. Hungerford, and E. F. Wicker. 1972. Insects and mites associated with western white pine blister rust cankers in Idaho. Canadian Entomol. 104:1713–1715.

Hanover, J. W. 1966. Tree improvement for disease resistance in western United States and Canada. Pages 53–66 *in* Breeding pest resistant trees. Proc. NATO-IUFRO Sym., Penn. St. Univ. 1964. Pergamon Press, Oxford, England. 505 pp.

Hatch, M. H. 1961. The beetles of the Pacific Northwest. Part III: Pselaphidae and Diversicornia 1. Univ. of Washington Press, Seattle. 503 pp.

Hiratsuka, Y., and J. M. Powell. 1976. Pine stem rusts of Canada. Canada Dep. Environ., For. Serv., Forestry Tech. Rep. 4. 83 pp.

Hiratsuka, Y., A. Tsuneda, and L. Sigler. 1979. Occurrence of *Scytalidium uredinicola* on *Endocronartium harknessii* in Alberta, Canada. Plant. Dis. Rept. 63:512–513.

Hoff, J. R., and G. I. McDonald. 1972. Stem rusts of conifers and the balance of nature. Pages 525–536 *in* Biology of rust resistance in forest trees. Proc. NATO-IUFRO Adv. Study Inst., Moscow, Idaho, 1969. USDA For. Serv. Misc. Publ. 1221. 681 pp.

Hubert, E. E. 1923. The life history of *Cronartium coleosporioides*. Unpublished manuscript. Div. For. Dis. Res., Washington Off. For. Serv. 76 pp.

Hungerford, R. D. 1977. Natural inactivation of blister rust cankers on western white pine. For. Sci. 23:343–350.

Hunt, R. S. 1978. Slugs feeding on *Cronartium* in British Columbia. Canadian For. Serv. Res. Note 34:21.

Kimmey, J. W. 1969. Inactivation of lethal-type blister rust cankers on western white pine. J. For. 67:296–299.

Krebill, R. G. 1968. *Cronartium comandrae* in the Rocky Mountain States. USDA For. Serv., Intermt. For. and Range Expt. Sta., Res. Pap. INT-40, 28 pp.

Kuhlman, E. G. 1981a. Mycoparasite effects of *Scytalidium uredinicola* on aeciospore production and germination of *Cronartium quercuum* sp. *fusiforme*. Phytopathology 71:186–188.

———. 1981b. Parasite interaction with sporulation by *Cronartium quercuum* subsp. *fusiforme* on loblolly and slash pine. Phytopathology 71:348–350.

Kuhlman, E. G., J. W. Carmichael, and T. Miller. 1976. *Scytalidium uredinicola* a new mycoparasite of *Cronartium fusiforme* on *Pinus*. Mycologia 68:1188–1194.

Kuhlman, E. G., and T. Miller. 1976. Occurrence of *Tuberculina maxima* on fusiform rust galls in the southeastern United States. Plant Dis. Rept. 60:627–629.

Leaphart, C. D., and E. F. Wicker. 1968. The ineffectiveness of cycloheximide and phytoactin as chemical controls of the blister rust disease. Plant Dis. Rept. 52:6–10.

LeConte, T. L. 1879. The Coleoptera of the alpine Rocky Mountain Regions—Part II. Bull. U.S. Geol. Survey 5(3,XXV):499–513.

MERKEL, E. P. 1958. *Dioryctria* cone moth attack as related to cone rust of slash pine in North Florida. J. For. 56:651.

MIELKE, J. L. 1933. *Tuberculina maxima* in western North America. Phytopathology 23:299–305.

______. 1935. Rodents as a factor in reducing aecial sporulation of *Cronartium ribicola*. J. For. 33:994–1003.

MIELKE, J. L., AND R. S. PETERSON. 1967. Albino *Peridermium harknessii* in ponderosa pine. Plant Dis. Rept. 51:306–509.

MYREN, D. T. 1964. Insects and fungi associated with *Cronartium fusiforme*-infected tissue and comparisons of the strength of infected and healthy wood. Phytopathology 54:902.

NIGHSWANDER, J. E., AND R. F. PATTON. 1965. The epidemiology of the jack pine-oak gall rust (*Cronartium quercuum*) in Wisconsin. Canadian J. Bot. 43:1561–1581.

PARSONS, C. T. 1967. North American Nitidulidae (Coleoptera) IV. *Epuraea* associated with fungi on pine and oak. Canadian Entomol. 99:734–737.

PETERSON, G. W. 1973. Dispersal of aeciospores of *Peridermium harknessii* in central Nebraska. Phytopathology 63:170–172.

PETERSON, R. S. 1959. Pine gall rust in the Rocky Mountains. Dissertation. Univ. of Michigan. Diss. Abstr. 20(5)1557, 111 pp.

______. 1966. Limb rust damage to pine. USDA For. Serv., Intermt. For. and Range Expt. Sta., Res. Pap. INT-31, 10 pp.

______. 1968. Limb rust of pine: the causal fungi. Phytopathology 58:309–315.

PETERSON, R. S., AND F. F. JEWELL. 1968. Status of American stem rusts of pine. Ann. Rev. Phytopathology 6:23–40.

POWELL, J. M. 1971a. Fungi and bacteria associated with *Cronartium comandrae* on lodgepole pine in Alberta. Phytoprotection 52:45–51.

______. 1971b. Occurrence of *Tuberculina maxima* on pine stem rusts in western Canada. Canadian Plant Dis. Surv. 51:83–85.

______. 1971c. Incidence and effect of *Tuberculina maxima* on cankers of the pine stem rust, *Cronartium comandrae*. Phytoprotection 52:104–111.

______. 1971d. The arthropod fauna collected from the comandra blister rust, *Cronartium comandrae* on lodgepole pine in Alberta. Canadian Entomol. 103:908–918.

______. 1971e. Additional records of *Mycodiplosis* larvae (Diptera: Cecidomylidae) feeding on rust fungi. Canadian Plant Dis. Surv. 51:86–87.

______. 1974. The role of natural biological agents in controlling a pine stem rust (*Cronartium comandrae*). Blue Jay 32:75–79.

POWELL, J. M., H. R. WONG, AND J. C. E. MELVIN. 1972. Arthropods collected from stem rust cankers of hard pines in western Canada. Canada Dept. Environ., Canadian For. Serv., Northern For. Res. Centre, Edmonton, Alberta. Rep. NOR-X-42, 19 pp.

SNELL, W. H. 1919. Observations on the relation of insects to the dissemination of *Cronartium ribicola*. Phytopathology 9:451–464.

TOKO, H. V., D. A. GRAHAM, C. E. CARLSON, AND D. E. KETCHAM. 1967. Effect of past *Ribes* eradications on controlling white pine blister rust in northern Idaho. Phytopathology 57:1010.

TRUE, R. P. 1938. Gall development on *Pinus sylvestris* attacked by the Woodgate *Peridermium*, and morphology of the parasite. Phytopathology 28:24–49.

TSUNEDA, A., AND Y. HIRATSUKA. 1979. Mode of parasitism of mycoparasite, *Cladosporium gallicola*, on western gall rust, *Endocronartium harknessii*. Canadian J. Plant Pathol. 1:31–36.

______. 1980. Parasitization of pine stem rust fungi by *Monocillium nordinii*. Phytopathology 70:1101–1103.

TSUNEDA, A., Y. HIRATSUKA, AND P. T. MARUYAMA. 1980. Hyperparasitism of *Scytalidium uredinicola* on western gall rust, *Endocronartium harknessii*. Canadian J. Bot. 58:1154–1159.

WILLIAMS, R. E. 1972. Fungi associated with blister rust cankers on western white pine. Dissertation. Washington State Univ. 125 pp. Xerox Univ. Microfilms, Ann Arbor, Mich., No. 72-31308. Diss. Abstr. 33/05-B, p. 2434.

WOLLENWEBER, H. W. 1934. *Fusarium bactridioides* sp. *nov.* associated with *Cronartium*. Science 79(2060):572.

VAN ARSDEL, E. P. 1961. Growing white pine in the Lake States to avoid blister rust. USDA For. Serv. Lake States For. Exp. Sta., Pap. 92, 11 pp.

WONG, H. R. 1972. *Dioryctria banksiella* (Lepidoptera: Pyralidae) in the western gall rust, *Endocronartium harknessii* (Basidiomycetes: Uredinales). Canadian Entomol. 104:251–255.